

# Assessing Multivariate Constraints to Evolution across Ten Long-Term Avian Studies

Celine Teplitsky<sup>1\*</sup>, Maja Tarka<sup>2</sup>, Anders P. Møller<sup>3</sup>, Shinichi Nakagawa<sup>4</sup>, Javier Balbontin<sup>5</sup>, Terry A. Burke<sup>6</sup>, Claire Doutrelant<sup>7</sup>, Arnaud Gregoire<sup>7</sup>, Bengt Hansson<sup>2</sup>, Dennis Hasselquist<sup>2</sup>, Lars Gustafsson<sup>8</sup>, Florentino de Lope<sup>9</sup>, Alfonso Marzal<sup>9</sup>, James A. Mills<sup>10</sup>, Nathaniel T. Wheelwright<sup>11</sup>, John W. Yarrall<sup>12</sup>, Anne Charmantier<sup>7</sup>

1 Département Ecologie et Gestion de la Biodiversité UMR 7204 CNRS/MNHN/UPMC, Muséum National d'Histoire Naturelle, Paris, France, 2 Department of Biology, Lund University, Ecology Building, Lund, Sweden, 3 Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Université Paris-Sud, Orsay, France, 4 Department of Zoology, University of Otago, Dunedin, New Zealand, 5 Department of Zoology, Biology Building, University of Seville, Seville, Spain, 6 Department of Animal and Plant Sciences, University of Sheffield, Sheffield, United Kingdom, 7 Centre d'Ecologie Fonctionnelle et Evolutive UMR 5175 CNRS, Montpellier, France, 8 Department of Animal Ecology, Evolutionary Biology Center, Uppsala University, Uppsala, Sweden, 9 Departamento de Zoología, Universidad de Extremadura, Badajoz, Spain, 10 Corning, New York, United States of America, 11 Department of Biology, Bowdoin College, Brunswick, Maine, United States of America, 12 Lincoln, Christchurch, New Zealand

## Abstract

*Background:* In a rapidly changing world, it is of fundamental importance to understand processes constraining or facilitating adaptation through microevolution. As different traits of an organism covary, genetic correlations are expected to affect evolutionary trajectories. However, only limited empirical data are available.

*Methodology/Principal Findings:* We investigate the extent to which multivariate constraints affect the rate of adaptation, focusing on four morphological traits often shown to harbour large amounts of genetic variance and considered to be subject to limited evolutionary constraints. Our data set includes unique long-term data for seven bird species and a total of 10 populations. We estimate population-specific matrices of genetic correlations and multivariate selection coefficients to predict evolutionary responses to selection. Using Bayesian methods that facilitate the propagation of errors in estimates, we compare (1) the rate of adaptation based on predicted response to selection when including genetic correlations with predictions from models where these genetic correlations were set to zero and (2) the multivariate evolvability in the direction of current selection to the average evolvability in random directions of the phenotypic space. We show that genetic correlations on average decrease the predicted rate of adaptation by 28%. Multivariate evolvability in the direction of current selection was systematically lower than average evolvability in random directions of space. These significant reductions in the rate of adaptation and reduced evolvability were due to a general nonalignment of selection and genetic variance, notably orthogonality of directional selection with the size axis along which most (60%) of the genetic variance is found.

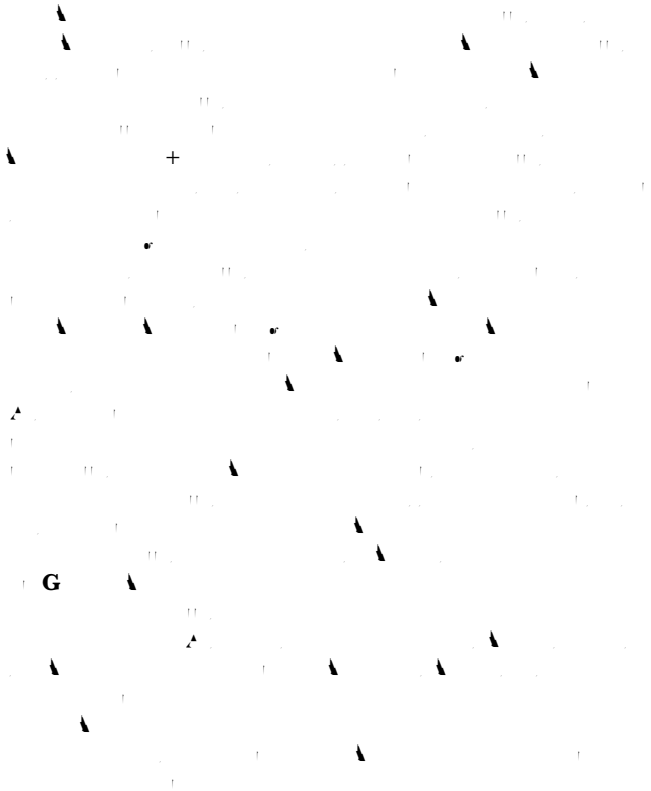
*Conclusions:* These results suggest that genetic correlations can impose significant constraints on the evolution of avian morphology in wild populations. This could have important impacts on evolutionary dynamics and hence population persistence in the face of rapid environmental change.

1. The first part of the document discusses the importance of maintaining accurate records of all transactions and activities related to the business. It emphasizes the need for transparency and accountability in financial reporting.

>  $\frac{1}{2} \frac{d}{dt} \left( \frac{1}{2} m v^2 \right) = \frac{1}{2} m v \frac{dv}{dt}$

Estimation of the additive genetic (co)variance matrix

**G**



$$y = \mu + \lambda + Z + Z + Z + \dots \quad (1)$$



$y \sim N(0, G \otimes A)$

**A**

**G**

Estimating selection



1. The first part of the text discusses the importance of maintaining accurate records of all transactions, including sales, purchases, and expenses. This is essential for ensuring the integrity of the financial statements and for providing a clear audit trail.

2. The second part of the text focuses on the need for transparency and accountability in financial reporting. This involves providing detailed disclosures of all significant transactions and events, as well as the methods used to estimate and measure financial performance.

3. The third part of the text emphasizes the importance of maintaining proper internal controls to prevent and detect errors and fraud. This includes implementing strong segregation of duties, regular reconciliations, and a robust system of internal audits.

4. The fourth part of the text discusses the need for ongoing monitoring and evaluation of the financial reporting process. This involves regularly reviewing the effectiveness of internal controls and making adjustments as needed to ensure the accuracy and reliability of the financial statements.

5. The fifth part of the text concludes by highlighting the importance of maintaining a strong relationship with external auditors. This involves providing them with all necessary information and documentation, and working closely with them to address any issues or concerns that may arise during the audit process.

**G**

Table 4. Estimates of mean standardized traits interval.

	Blue tit - Muro	Blue tit - Pirin
	posterior mode	posterior mode
	Lower	Upper 95%CI
Wing	0.018	0.013
Tarsus	0.041	0.043
Mass	0.075	0.079
Bill	0.045	0.028
Wing:Tarsus	0.01	0.012
Wing:Mass	0.012	0.012
Wing:Bill	0.008	0.007
Tarsus:Mass	0.021	0.029
Tarsus:Bill	0.019	0.013
Mass:Bill	0.032	0.017

IA-evolvabilities were higher for mass than for other characters (doi:10.1371/journal.pone.0090444.t004)

estimated  $V_A \times 100$

	Blue tit - Muro	Blue tit - Pirin
	posterior mode	posterior mode
	Lower	Upper 95%CI
Wing	0.018	0.013
Tarsus	0.041	0.043
Mass	0.075	0.079
Bill	0.045	0.028
Wing:Tarsus	0.01	0.012
Wing:Mass	0.012	0.012
Wing:Bill	0.008	0.007
Tarsus:Mass	0.021	0.029
Tarsus:Bill	0.019	0.013
Mass:Bill	0.032	0.017

on a linear scale [40].

see Blue tit populations with their 95% confidence

	Blue tit - Muro	Blue tit - Pirin
	posterior mode	posterior mode
	Lower 95%CI	Upper 95%CI
Wing	0.018	0.013
Tarsus	0.041	0.043
Mass	0.075	0.079
Bill	0.045	0.028
Wing:Tarsus	0.01	0.012
Wing:Mass	0.012	0.012
Wing:Bill	0.008	0.007
Tarsus:Mass	0.021	0.029
Tarsus:Bill	0.019	0.013
Mass:Bill	0.032	0.017

characters were measured on a linear scale [40].

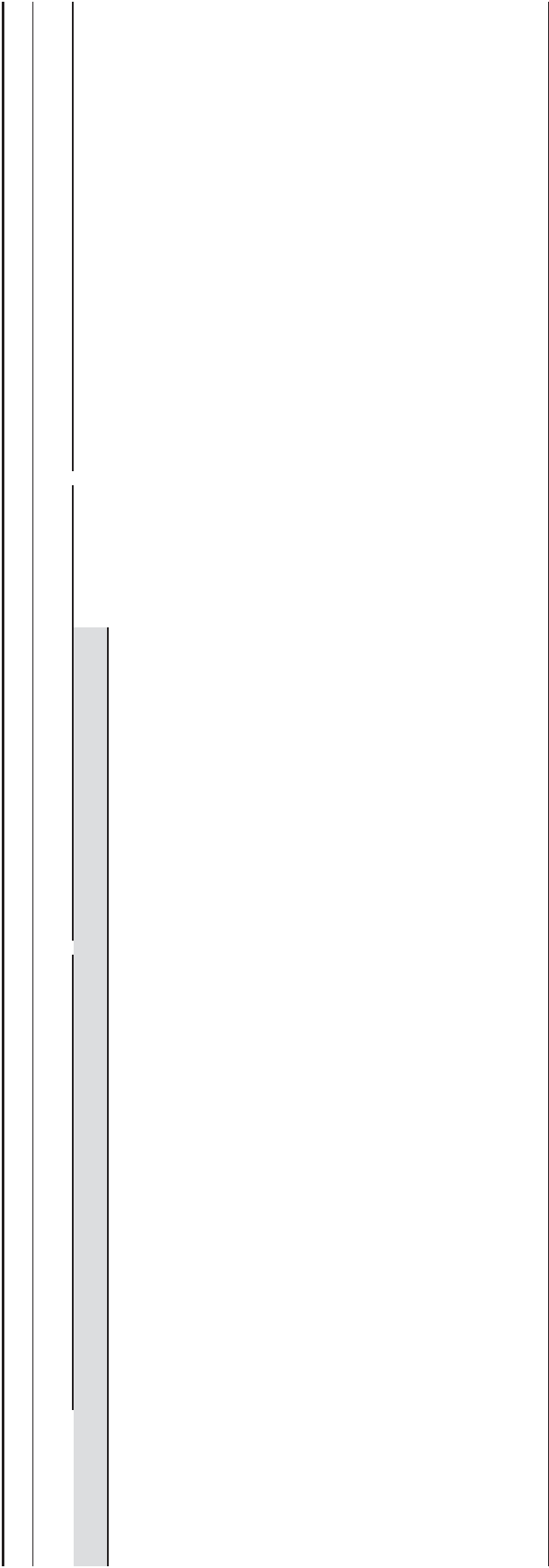
$$\beta = \frac{\mathbf{\beta}^T \mathbf{G} \mathbf{\beta}}{\|\mathbf{\beta}\|^2} \quad (4)$$



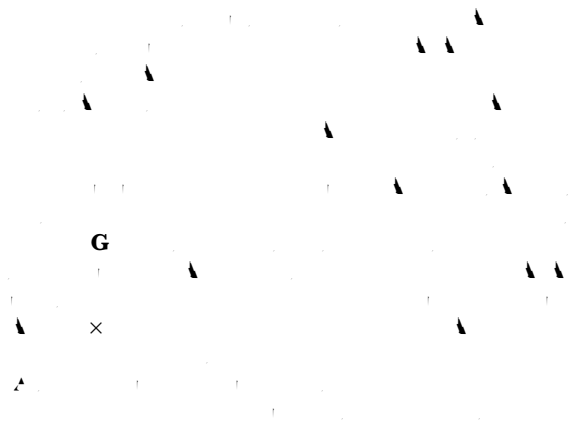
Table 7. Estimates of directional and non-linear selection gradients for the Red-billed gull, Great reed warbler, and Barn swallow - Back intervals.

	Red-billed gull			Great reed warbler			Barn swallow - Back		
	posterior mode	Low 95%CI	Up 95%CI	posterior mode	Low 95%CI	Up 95%CI	posterior mode	Low 95%CI	Up 95%CI
$\parallel \beta \parallel$	4.22	1.94	7.24	5.23	2.53	8.17	0.54		
Wing	1.14	-2.75	5.9	-0.09	-3.79	4.12	0.33		
Tarsus	1.86	-1.12	4.39	4.04	1.45	7.69	0.12		
Mass	-1.15	-2.39	0.32	-1.78	-3.02	-0.51	0.08		
Bill	1.86	-1.83	5.35	0.58	-1.48	1.96	0.15		
Wing <sup>2</sup>	139.96	-27.15	243.35	15.61	-107.1	233.37	-13.47		
Tarsus <sup>2</sup>	29.1	-33.29	88.21	24.88	-61.64	128.76	2.78		
Mass <sup>2</sup>	9.26	<b>2.7895</b>	<b>2.423355(35)-7</b>						









Natural selection on morphology

...  $\beta$  ...

### Discussion

...  $\beta$  ...

